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Synonymy of the Genus *Marimbonda* Richards, 1978, with *Leipomeles* Möbius, 1856 (Hymenoptera: Vespidae; Polistinae), and a New Key to the Genera of Paper Wasps of the New World

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ABSTRACT

The paper wasp genus *Marimbonda* Richards, 1978, is synonymized with *Leipomeles* Möbius, 1856, n.syn. A key to all the currently recognized paper wasp genera in the Western Hemisphere is provided.

INTRODUCTION

The paper wasp genus *Marimbonda* was described by Richards (1978) for two species: the type species *M. albogrisea* Richards, 1978, and *M. pusilla* (Ducke, 1904). The recognition of this new genus was due primarily to the nest architecture of the new species *M. albogrisea*. The single nest collected was astelocytarus (Richards and Richards, 1951: 6): the comb lacking any petiole, with the cells constructed on a flat surface

and an envelope covering the comb. Richards (1978: 10) keyed the new genus out with those genera also bearing a stout, curved bristle on the third segment of the labial palpus (figs. 1–2), and among these the genera sharing reduction in the palpal formula to five-segmented maxillary palpi and three-segmented labial palpi (fig. 1). However, his dendrogram (Richards, 1978: fig. 40) showed *Marimbonda* as intermediate between these genera and a group clade including other genera with astelocytarus nest architecture.

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Richards (1978: 201) stated: "The genus whose relationships are shown in the dendrogram . . . and in the key . . . does not seem to be at all allied to the others which make astelocytarus nests (*Synoeca*, *Metapolybia*, and *Clypearia*) and while it should probably be placed somewhere near the others which have the curved bristle on the labial palpus, it does not seem to be close to any of them."

The other genera with the bristle on the third labial palpomere are *Pseudopolybia*, *Parachartergus*, *Chartergellus*, *Nectarinella*, and *Leipomeles*. In previous cladistic analyses of paper wasp genera (Carpenter, 1991; Wenzel and Carpenter, 1994) these genera were shown to form a monophyletic group including *Marimbonda*; that bristle is a synapomorphy. Within this clade, *Marimbonda* and *Leipomeles* are sister-groups. A morphological synapomorphy is the similar form of the first metasomal segment (conically petiolate; figs. 3–4), while a possible synapomorphy in nest architecture is a central furrow built in the lines of construction of the envelope.

In the present work, *Marimbonda* and *Leipomeles* are synonymized. Although it is possible to adduce morphological apomorphies to support each genus as monophyletic (e.g., *Leipomeles* has the first metasomal segment forming a longer, relatively narrower petiole, fig. 4; *Marimbonda* has the hindwing with vein Cu_1 as long as $cu-a$, fig. 5, vs. Cu_1 shorter than $cu-a$ in *Leipomeles*, fig. 6), these are all minor features, relative both to the features shared by these genera and features defining other paper wasp genera. More significantly, *Marimbonda* was recognized as a genus in the first place because of its nest architecture, but its astelocytarus design is less important than other features of the nest that it shares with *Leipomeles* (Wenzel and Carpenter, 1994). The astelocytarus nest obscured the relationships of *Marimbonda* when that genus was described—in fact was misleading, as seen from Richards' placement of the genus on his dendrogram. Moreover, as will be shown, astelocytarus nests do not in fact separate *Marimbonda* from *Leipomeles*.

After discussion of taxonomic history and further explication of the rationale for the synonymy, a new key to the paper wasp gen-

era is provided, which will cover all the taxa found in the New World.

TAXONOMIC HISTORY

The present generic classification of New World Polistinae owes its basic form to the work of Adolpho Ducke. A century ago, working at the Museu Goeldi in Belem, he revised the classification then prevailing, and his views were especially informed by his own extensive field work in Amazonian Brazil. Prior to Ducke the classification used was basically that in the last worldwide monograph (de Saussure, 1853–1858), which itself was a refinement of Lepeletier's (1836) classification, who began the recognition of numerous genera for Polistinae. Polistinae were separated from other Vespidae (as the Linnaean genus *Vespa*) by Latreille (1802), who described two genera, *Polistes* and *Epipona*. Between the time of Latreille and Lepeletier just a few isolated genera were described (Kirby, 1826: *Cyclostoma*²; Guérin-Méneville, 1831: *Ropalidia*; Perty, 1833: *Brachygastra*), but Lepeletier described five genera: *Agelaia*, *Apoica*, *Chartergus*, *Polybia*, and *Rhopalidia*.³ Between the time of Lepeletier and de Saussure again just a couple of genera were added (White, 1841: *Anthreneida*,⁴ *Myrapetra*⁵). De Saussure (1852) added *Synoeca* and de Saussure (1853–1858) *Raphigaster*⁶ and *Mischocyttarus*. Subsequent to de Saussure's work a few more genera accumulated (Möbius, 1856: *Leipomeles*; Gribodo, 1892: *Paraicaria*⁷; H. von Ihering, 1896: *Pseudopolybia*⁸; Fox, 1898: *Charterginus*).

Working on the fauna of Pará, Ducke

² Junior homonym of *Cyclostoma* Lamarck, 1799; replaced by *Gyrostoma* Kirby, 1828; now a subgenus of *Polistes* (Carpenter, 1996).

³ Suppressed by Opinion 1051 of the International Commission on Zoological Nomenclature (1976); the name *Angiopolybia* Araujo, 1946, is now used for this genus.

⁴ Synonymized with *Ropalidia* Guérin-Méneville, 1831, by Kojima (1997).

⁵ Now a subgenus of *Polybia* (Richards, 1978).

⁶ Junior homonym of *Raphigaster* Laporte, 1832; replaced by *Belonogaster* de Saussure, 1853.

⁷ Synonymized with *Ropalidia* Guérin-Méneville, 1831, by Kojima (1997).

⁸ Junior homonym of *Pseudopolybia* de Saussure, 1863; junior synonym of *Kappa* de Saussure, 1854, a subgenus of *Mischocyttarus*.

(1904) at first followed de Saussure's classification, adding just one genus, *Megacanthopus*.⁹ But shortly thereafter, Ducke (1905a) radically revised the generic classification of the South American Polistinae. De Saussure had recognized eight genera of Polistinae in the Neotropics; Ducke (1905a) recognized 18. In particular, he split up the genera *Chartergus* and *Polybia*, both quite heterogeneous in his 1904 study. With respect to *Chartergus* he added the genus *Parachartergus*, a genus described shortly before by R. von Ihering (1904), as well as the new genus *Pseudochartergus*. In addition to *Polybia*, he raised to generic rank *Clypearia* de Saussure, 1854, and *Charterginus* Fox, 1898, treated by him as subgenera of *Polybia* in 1904; recognized *Leipomeles* Möbius, 1856, treated by him as a synonym of *Polybia* in 1904; and added the new genera *Synoecoides* and *Metapolybia*.

Marimbonda pusilla was originally described in the genus *Chartergus* by Ducke (1904), from Belem and Oyapoc in Brazil. When Ducke (1905a) began to revise the generic classification, he transferred *C. pusillus* to *Parachartergus*. Möbius (1856) first used the palpal formula as a taxonomic character, when describing the genus *Leipomeles*, and R. von Ihering (1904: 129) cited this example in justifying his new genus. *Parachartergus* was described as monotypic, distinguished from *Chartergus* by labial palpi being three-segmented not four-segmented. Ducke (1905a, 1905b), however, argued that many species hitherto considered as *Chartergus* had the fourth labial palpomere rudimentary, and that therefore they could not be separated generically from *Parachartergus*. As defining characters of *Parachartergus* were cited the thick, long, curved bristle before the extremity of the labial palpus, and nests, where known, all stelocytarus calyptodomous (terminology of de Saussure, 1853–1858, meaning petiole combs covered with an envelope and free of the latter). Interestingly, Ducke (1904: 357) had refused to accept *Leipomeles* as a genus, deriding the importance of the palpi as a generic character: “Mas como hoje já passou o tempo em que se ba-

seava generos novos sobre pequenas diferenças no aparelho buccal . . .”. Under his changed view (Ducke, 1905a), the five-segmented maxillary palpi was the key character state separating *Leipomeles* from *Parachartergus*, both of which had the bristle on the labial palpus and stelocytarus calyptodomous nests—but he did not recognize that two species he placed in *Parachartergus* also have that condition, namely *pusillus* and *ater* (de Saussure).¹⁰ Ducke (1905a, 1905b) recognized four species groups in *Parachartergus*, only one of which had the fourth labial palpomere either rudimentary or lacking. That was his first group for species now placed in *Parachartergus* or *Chartergellus* Bequaert—species that, as far as is known, all have the labial palpi three-segmented, never with a rudimentary fourth segment. Ducke's (1905a, 1905b) three other species groups within *Parachartergus* were all stated to have the fourth segment of the labial palpus very distinct. That is correct for two of the groups, which are species now placed in *Pseudopolybia* de Saussure, but incorrect for his fourth group, which consisted solely of *pusillus*.

In 1914, Ducke transferred *pusillus* to *Pseudopolybia*, which was raised to generic rank by R. von Ihering (1913: 227; *Pseudopolybia* had been described as a division of *Polybia* by de Saussure, 1863). The species did not receive much further attention, although it was misidentified by Bequaert (1944), and following him Richards (*in* Richards and Richards, 1951), who used the name for *Leipomeles spilogastra* (Cameron) (see Carpenter, 1999: 9). Then Richards (1978: 202) studied a specimen, which he designated as lectotype, and transferred the species to his new genus, *Marimbonda*.

Ducke's (1914) definitive generic classification for neotropical Polistinae recognized 20 genera, a number that was not augmented until Richards (1978), who recognized 24. Of Richards' four additional genera, two were elevations of subgenera described by Bequaert (1938: *Chartergellus*, *Nectarinella*), while two were new taxa, *Marimbonda* and *Occipitalia*. The latter was subsequently syn-

⁹ Now a subgenus of *Mischocyttarus* (Richards, 1941).

¹⁰ Preoccupied; the name has been replaced by *Chartergellus amazonicus* Richards, 1978.

onymized with *Clypearia* by Carpenter et al. (1996), who showed the single species included in *Occipitalia* to be intermediate in the morphological and nest architectural characters defining *Clypearia*. Other work subsequent to Richards (Raw, 1985; Carpenter and Wenzel, 1990; Carpenter et al., 2000) has led to a number of 22 presently recognized neotropical polistine genera. Synonymy of *Marimbonda* with *Leipomeles* now reduces that number to 21.

SYNONYMY

Leipomeles and *Marimbonda* share numerous morphological features that are certainly derived: the third segment of the labial palpus bearing a stout, curved bristle apically, reduction in the palpal formula to five-segmented maxillary palpi and three-segmented labial palpi, mesepisternum without dorsal groove, and first metasomal segment conically petiolate. The two genera are not keyed out together in Richards' key (1978: 10), but that is partly erroneous. Thus, the pronotal fovea is not "weak or absent" in *Leipomeles*; when present, it is as "strong" as other genera. Also contrary to the key, the anterior pronotal carina ("prominence") is in fact acute, and the metanotum in fact has a dorsal surface. The secondary spiracular entrance and propodeal valvula do not differ between *Leipomeles* and *Marimbonda*. This leaves the cuticle, which is less punctured and more shining in *Leipomeles* than *Marimbonda*, the form of the metasomal petiole which is more elongate in *Leipomeles* (cf. figs. 3 and 4), and the derived hindwing venation in *Marimbonda* (fig. 5). None of these features is as significant as the features shared by the two genera, and all are of less significance than the features by which other genera are differentiated (see key, below). Moreover, greater variation in all of these features is found within other genera: sharper differences in punctation occur in, for example, *Polybia*, *Protopolybia*, and *Ropalidia*; the form of the metasomal petiole is much more variable in, for example, *Mischocyttarus* and *Polybia*, and the difference between *Leipomeles* and *Marimbonda* is less than occurs within *Polistes*; and the hindwing venation is much more divergent within

Parapolybia and *Polybioides* (van der Vecht, 1966; Carpenter, 1999), with CuA vein separating from M+CuA distad of the insertion of the cu-a crossvein, instead of basad of the insertion of cu-a.

The chief justification for recognition of *Marimbonda* as a genus in any case was the asterlocyttarus nest architecture. Only the nest collected with the type series of *M. albogrisea* is definitely known; Wenzel (1998: 16) stated to have seen another nest he believed to be *Marimbonda*, but the identity was not certain. According to Martin Cooper (*in litt.*), who collected the nest identified in Wenzel (1998: fig. 23D) as *Marimbonda*, it was found in Colombia, and was abandoned. Cooper's initial identification was as a *Leipomeles* nest, but Wenzel assigned it to *Marimbonda* because the comb was sessile. As will be seen, that is no longer grounds for generic assignment.

As discussed by Wenzel and Carpenter (1994), the nests of *Marimbonda* and *Leipomeles* share several derived architectural components, including application of blots of colored pulp to the envelope, envelope with ridges parallel to the lines of construction, and envelope with a central, impressed, longitudinal furrow. That last character is evidently variably present within both genera according to Wenzel (1998), who keyed out both genera together. *Leipomeles* always nests on the undersides of leaves, whereas the nest of *Marimbonda* collected by Richards was on the trunk of a sapling. The putative nest of *Marimbonda* was on a leaf (see Wenzel, 1998: 16), but it may have been *Leipomeles*. That aside, the absence of a petiole on the comb of *Marimbonda* was the only consistent difference in nest architecture between *Leipomeles* and *Marimbonda*. The number of petioles has long been known to be variable in *Leipomeles*, from one to several, and their orientation with respect to the substrate (leaf veins) may be vertical or oblique. Petioles have always been thought to be present, but I have now seen nests of *Leipomeles dorsata* (Fabricius) that lack them. First, a nest was sent to me by James H. Hunt, along with adult wasps, collected in Costa Rica: Prov. Heredia, La Selva Biological Station, 18 Jan. 1991 (J. H. Hunt), nest no. CR91-2. The single comb was attached

to the underside of a leaf along the midrib not by a petiole, but rather by a low fibrous ridge that ran along the entire length of the comb. A hole in the ridge may possibly indicate fusion of originally separate structures, but if so these were ribbonlike rather than petiolate. Second, I have seen a nest at the Universidade de São Paulo in Ribeirão Preto, collected by Gabriel A. R. Melo in Brazil: Amazonas, Beruri, R. Purus, 16 Oct. 1991 (G. A. R. Melo), no. M89, along with adult wasps. The single comb was on the underside of a leaf of *Astrocaryum*, attached along its entire surface. Moreover, he collected another nest of this species in the same locality, identically attached along the entire surface.

Thus, *astelocytarus* combs may occur in *Leipomeles*, and the main justification for separating *Marimbonda* collapses. Accordingly, I am synonymizing these genera. The synonymy follows, and then a new key to the genera of Polistinae of the New World.

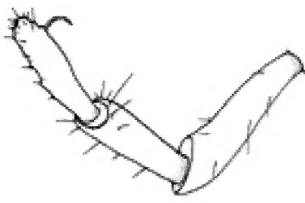
Genus *Leipomeles* Möbius

- Leipomeles* Möbius, 1856, Nester Gesell. Wespen: 25, genus.
- Type species: *Leipomeles lamellaria* Möbius, 1856 [= *Polistes dorsata* Fabricius, 1804], by monotypy.
- Lipomeles* Schulz, 1906, Spolia Hym.: 232. Unjustified emendation of *Leipomeles* Möbius.
- Marimbonda* Richards, 1978, Social Wasps Am.: v, 10, 201, genus. NEW SYNONYMY. Type species: *Marimbonda albogrisea* Richards, 1978, by original designation.

KEY TO THE GENERA OF NEW WORLD POLISTINAE

1. Metasomal segment I sub sessile, funnel-shaped in dorsal view (fig. 7); propodeum with orifice dorsally acute (fig. 7); pronotum with a carina posterior to the lateral fovea (fig. 9) tribe Polistini, *Polistes* Latreille
 - Metasomal segment I differently shaped, in dorsal view basally petiolate to long-petiolate or sessile with width greater than length (figs. 3–4, 8, 27, 29, 45–47); propodeum with orifice usually more broadly rounded dorsally (figs. 8, 45); pronotum if with carina and lateral fovea, then the carina is anterior to the fovea (fig. 10) or the two are not closely approximated (fig. 18) 2
2. Mid- and hindtarsi with third and fourth segments asymmetrical, inner lobe longer than outer lobe (fig. 11); forecoxa not dorsolaterally produced (fig. 13); metasomal segment I petiolate, not abruptly expanding posteriorly, in dorsal view with width half or less that of II, and at least twice as long as wide (fig. 8) tribe Mischocyttarini, *Mischocyttarus* de Saussure
 - Mid- and hindtarsi with third and fourth segments symmetrical (fig. 12); forecoxa usually dorsolaterally produced (fig. 14); metasomal segment I variously shaped tribe Epiponini, 3
3. Third labial palpomere with stout, recurved bristle apically (figs. 1, 2); female clypeus with square lateral lobes and sharply pointed apex (fig. 42) 4
 - Third labial palpomere without bristle; female clypeus variable 8
4. Head with occipital carina present (figs. 15–17) 5
 - Head without occipital carina (fig. 18–19) 6
5. Pronotum with dorsal carina sinuous in lateral view (figs. 10, 17); forewing with prestigma about as long as pterostigma (fig. 20) *Parachartergus* R. von Ihering
 - Pronotum without sinuous carina (figs. 16, 18–19); forewing with prestigma shorter than pterostigma (fig. 21) *Leipomeles* Möbius
6. Metanotum vertical posteriorly (fig. 18); scutellum angular in profile (fig. 18) *Nectarinella* Bequaert
 - Metanotum rounded, not vertical posteriorly (fig. 19); scutellum rounded in profile (fig. 19) 7
7. Mesepisternum without dorsal groove (fig. 18); maxillary palpi five-segmented and labial palpi (fig. 1) three-segmented *Chartergellus* Bequaert
 - Mesepisternum with dorsal groove present, at least as anterior trace (fig. 19); maxillary palpi six-segmented and labial palpi (fig. 2) four-segmented *Pseudopolybia* de Saussure
8. Pronotum without lateral fovea (figs. 22, 23) 9
 - Pronotum with lateral fovea (figs. 18, 40), sometimes shallow 15
9. Scutellum angled in profile (fig. 22); metanotum not projecting beyond scutellum posteriorly (figs. 22, 24); head with occipital carina present dorsolaterally (fig. 22); pronotum without pretegular carina (fig. 24) *Brachygastra* Perty

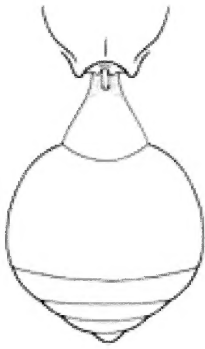
- Scutellum rounded in profile (fig. 23); projecting beyond scutellum posteriorly (figs. 23, 25); head with occipital carina present or absent; pronotum with pretegular carina (fig. 25) 10
10. Propodeum with dorsolateral carinae (fig. 26); metanotum with medial tubercle (fig. 26), sometimes weak; head with occipital carina present dorsolaterally (fig. 23) *Chartergus* Lepeletier
- Propodeum without carinae (figs. 27–29); metanotum without tubercle (figs. 27–29); head without occipital carina (fig. 29) 11
11. Forecoxa not dorsolaterally produced (fig. 13) 12
- Forecoxa dorsolaterally produced (fig. 14) 13
12. Propodeum posteromedially concave (fig. 28); body with some pale maculations, not metallic; head in lateral view with tempora narrower than eye at ocular sinus (figs. 48–49); clypeus longer than wide *Clypearia* Ducke
- Propodeum posteromedially convex (fig. 29); body without pale maculations, cuticle partly to entirely bluish metallic or yellowish with some bluish highlights; head in lateral view with tempora as wide or wider than eye at ocular sinus (figs. 16, 50); clypeus at most as long as wide *Synoeca* de Saussure
13. Clypeus apically emarginate (fig. 30); cuticle black, bare, and shining *Epipona* Latreille
- Clypeus apically bluntly pointed (fig. 31); cuticle not shining 14
14. Metasomal segment I in lateral view more flattened posteriorly (fig. 32), in dorsal view with maximum width 3× basal width *Asteloeca* Raw
- Metasomal segment I in lateral view convex posteriorly (fig. 33), in dorsal view with maximum width 2× basal width *Metapolybia* Ducke
15. Scutum with posterolateral lamella present adjoining tegula (fig. 34) 16
- Scutum with posterolateral lamella absent anteriorly, not adjoining tegula (fig. 35) 17
16. Ocelli enlarged, separated from eyes by less than an ocellar diameter (fig. 36); hindwing with jugal lobe reduced (fig. 38) *Apoica* Lepeletier
- Ocelli normal, separated from eyes by more than an ocellar diameter (fig. 37); hindwing with jugal lobe normal, not reduced (fig. 39) *Agelaia* Lepeletier
17. Mesepisternum with dorsal groove (fig. 40); female clypeus with square lateral lobes and sharply pointed apex (fig. 42) *Angiopolybia* Araujo
- Mesepisternum without dorsal groove (fig. 41); female clypeus with lateral lobes rounded (figs. 37, 43, 44) and apex bluntly pointed (fig. 37) or rounded (fig. 43) or truncate (fig. 44) 18
18. Metanotum produced posteromedially into elongate lobe overlapping the propodeum (fig. 45) *Protopolybia* Ducke
- Metanotum without posterior lobe 19
19. Metasomal segment I in dorsal view with short petiole, apically abruptly broadened, wider than half the width of segment II (fig. 46); head in lateral view with tempora much narrower than eye at ocular sinus (fig. 48); pronotum with anteromedial fovea *Charterginus* Fox
- Metasomal segment I in dorsal view differently shaped, narrowly petiolate to sessile (fig. 47); head in lateral view with tempora at least as wide as eye at ocular sinus (fig. 49), usually wider (fig. 50); pronotum without anteromedial fovea 20
20. Lateral ocelli almost as far apart as distance from each to eyes (fig. 51); eyes bristled (fig. 51); metasomal segment I not petiolate in dorsal view *Protonectarina* Ducke
- Lateral ocelli closer to each other than either is to eyes (fig. 37); eyes usually not bristled; metasomal segment I usually petiolate in dorsal view *Polybia* Lepeletier



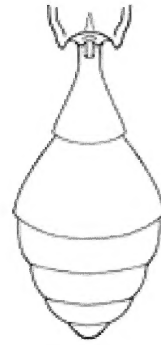
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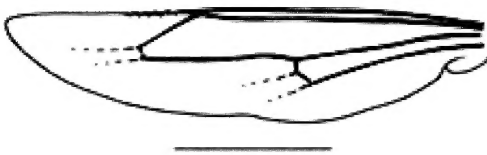
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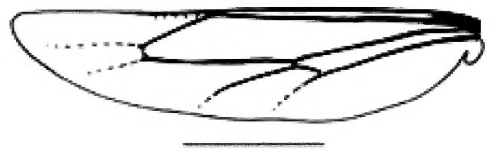
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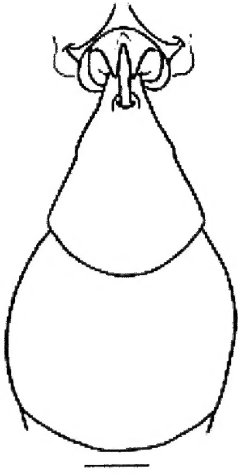


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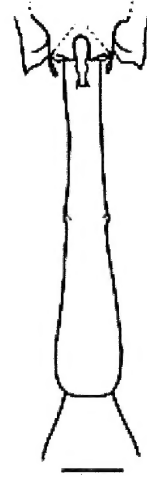


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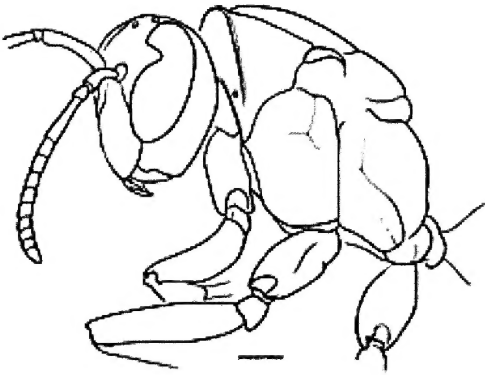
Figs. 1–6. Neotropical Polistinae. 1–2. Labial palpus. 1. *Chartergellus nigerrimus* Richards. 2. *Pseudopolybia compressa* (de Saussure). 3–4. Metasoma in dorsal view. 3. *Marimbonda albogrisea* Richards. 4. *Leipomeles dorsata* (Fabricius). 5–6. Hindwing. 5. *Marimbonda albogrisea* Richards. 6. *Leipomeles dorsata* (Fabricius). All scale bars are 1.0 mm.



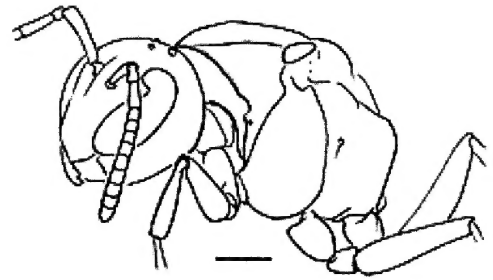
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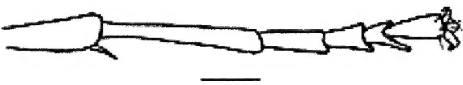
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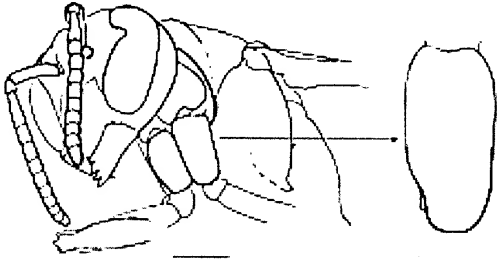


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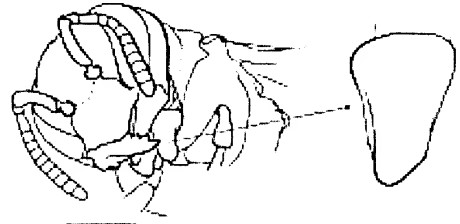


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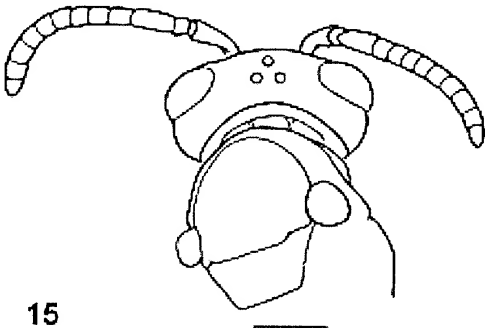
Figs. 7-12. Neotropical Polistinae. 7-8. Metasomal terga I and II in dorsal view. 7. *Polistes consobrinus* de Saussure. 8. *Mischocyttarus rotundicollis* (Cameron). 9-10. Head and mesosoma in anterolateral view. 9. *Polistes consobrinus* de Saussure. 10. *Parachartergus fraternus* (Gribodo). 11-12. Hindtarsus. 11. *Mischocyttarus rotundicollis* (Cameron). 12. *Brachygastra augusti* (de Saussure). All scale bars are 1.0 mm.



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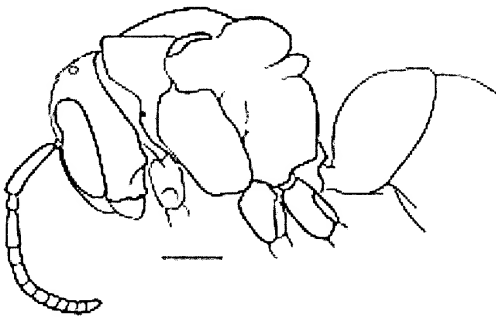
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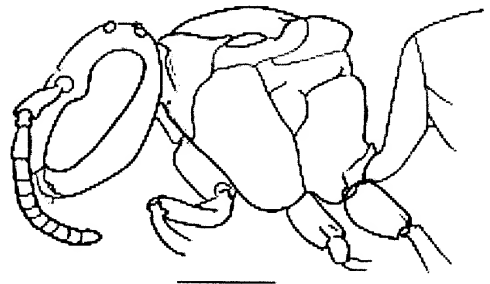
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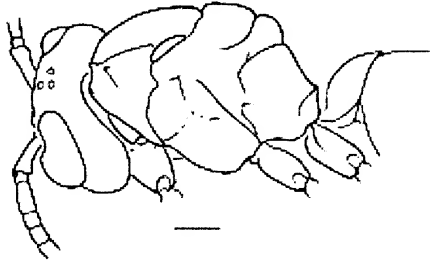


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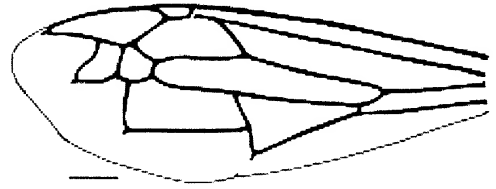


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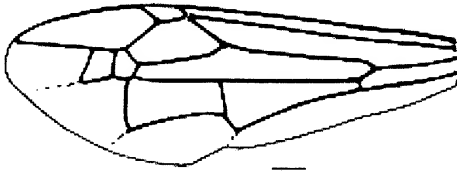
Figs. 13–18. Neotropical Polistinae. **13–14.** Head and prothorax in oblique frontal view, with procoxa set off in lateral view. **13.** *Mischocyttarus rotundicollis* (Cameron). **14.** *Brachygastra augusti* (de Saussure). **15–16.** *Agelaia multipicta* (Haliday). **15.** Head and mesosoma in oblique posterior view. **16.** Lateral view. **17.** *Parachartergus fraternus* (Gribodo), posterolateral view. **18.** *Nectarinella championi* (Dover), head and mesosoma in lateral view. All scale bars are 1.0 mm.



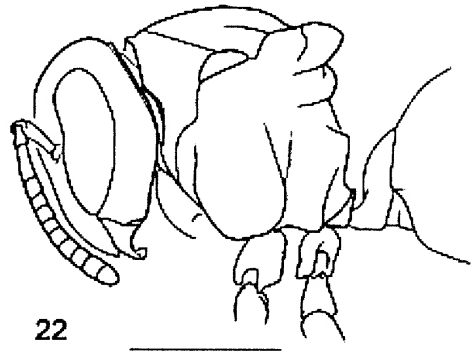
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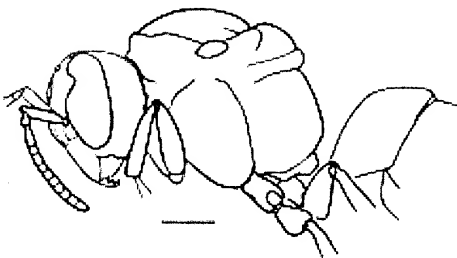
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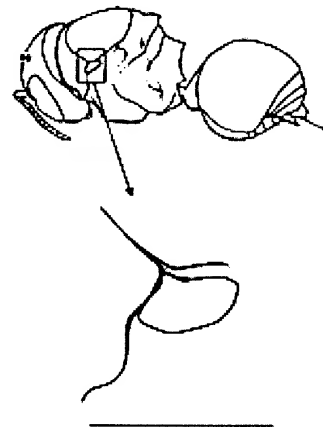
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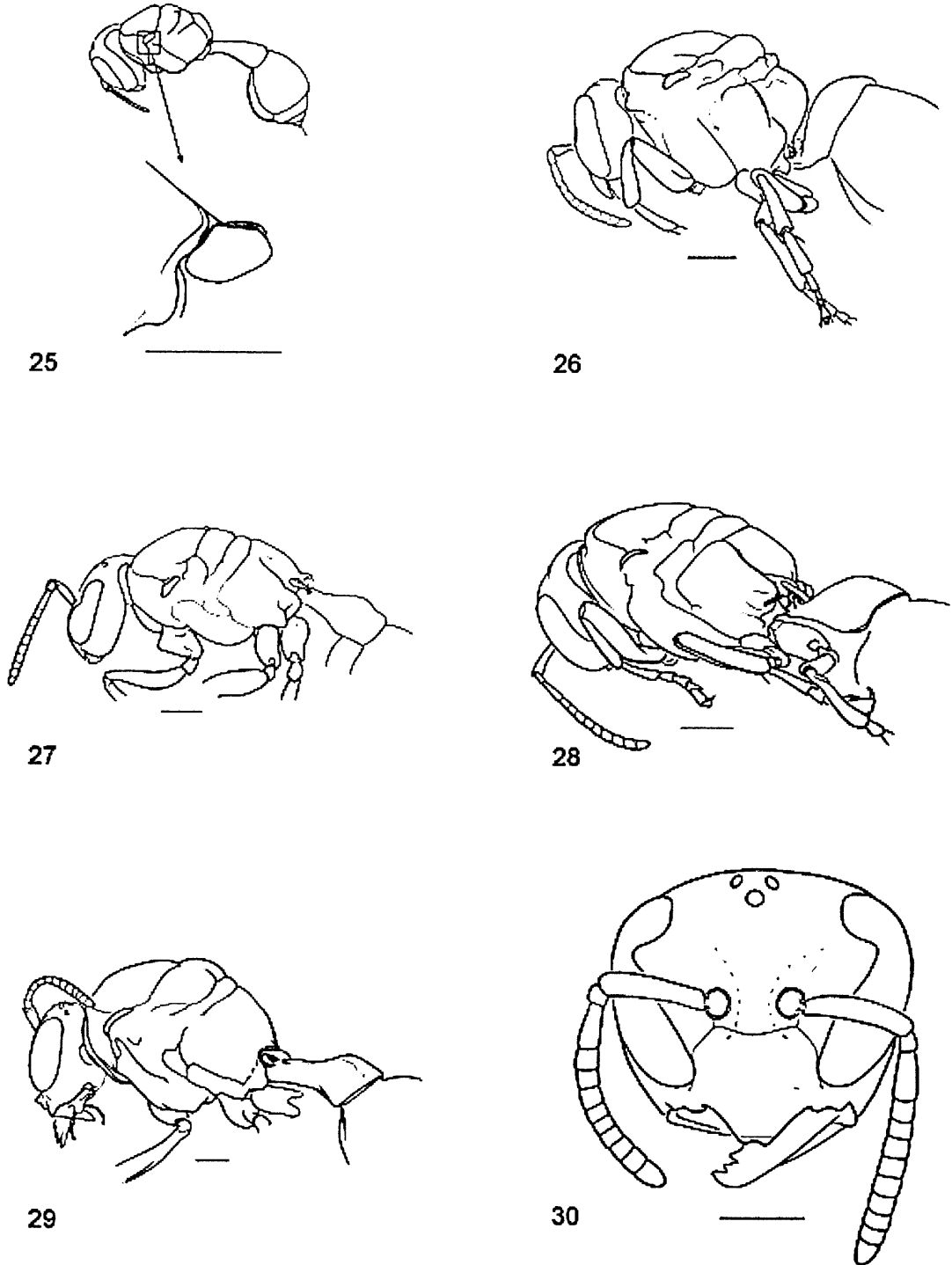


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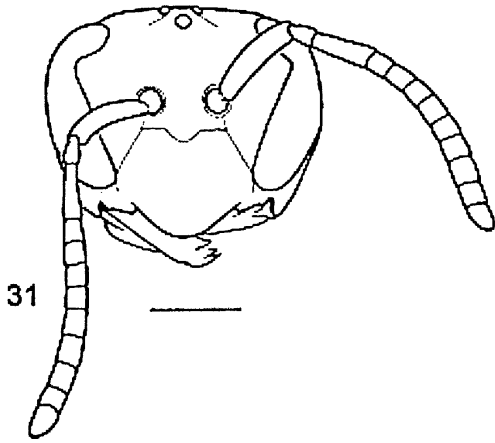


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Figs. 19–24. Neotropical Polistinae. **19.** *Pseudopolybia vespiceps* (de Saussure), head and mesosoma in oblique lateral view. **20–21.** Forewing. **20.** *Parachartergus fraternus* (Gribodo). **21.** *Angiopolybia obidensis* (Ducke). **22–23.** Head and mesosoma in lateral view. **22.** *Brachygastra augusti* (de Saussure). **23.** *Chartergus artifex* (Christ). **24.** *Brachygastra augusti* (de Saussure), oblique posterolateral view, with pronotum and tegula set off. All scale bars are 1.0 mm.



Figs. 25–30. Neotropical Polistinae. **25.** *Epipona guerini* (de Saussure), oblique posterolateral view, with pronotum and tegula set off. **26–29.** Oblique posterolateral view. **26.** *Chartergus artifex* (Christ). **27.** *Asteloeca traili* (Cameron). **28.** *Clypearia sulcata* (de Saussure). **29.** *Synoeca cyanea* (Fabricius). **30.** *Epipona guerini* (de Saussure), head in frontal view. All scale bars are 1.0 mm.



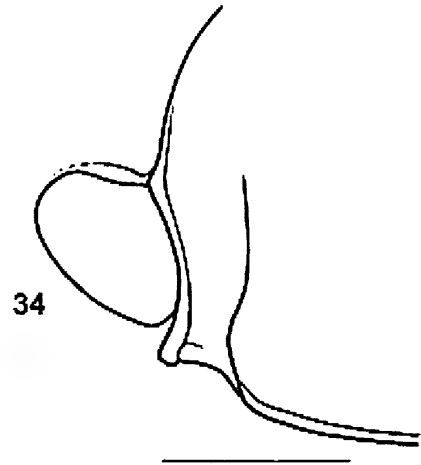
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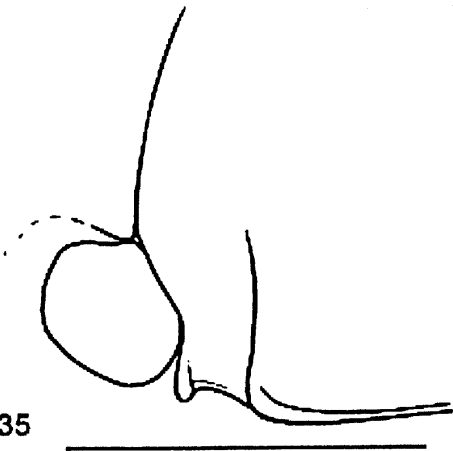
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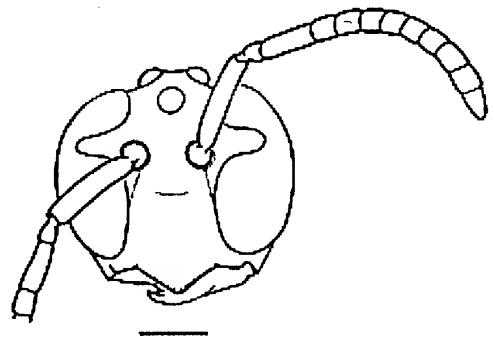
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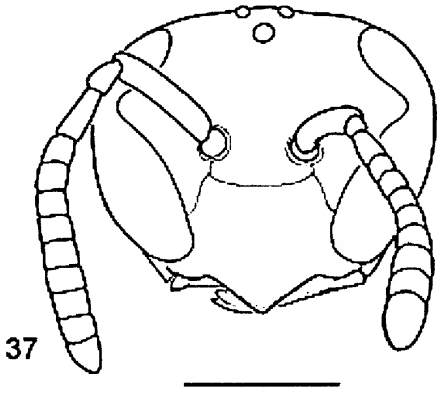


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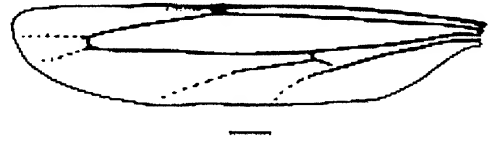


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Figs. 31–36. Neotropical Polistinae. **31.** *Asteloeca traili* (Cameron), head in frontal view. **32–33.** lateral view. **32.** *Asteloeca traili* (Cameron). **33.** *Metapolybia cingulata* (Fabricius). **34–35.** Scutum and tegula in dorsal view. **34.** *Apoica pallens* (Fabricius). **35.** *Polybia bistriata* (Fabricius). **36.** *Apoica pallens* (Fabricius), head in frontal view. All scale bars are 1.0 mm.



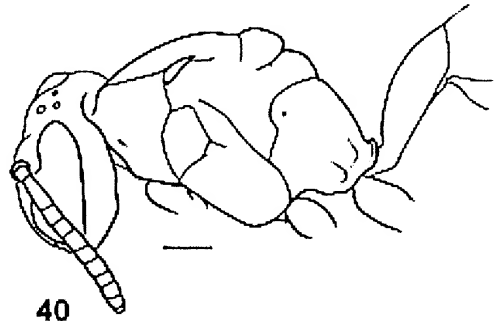
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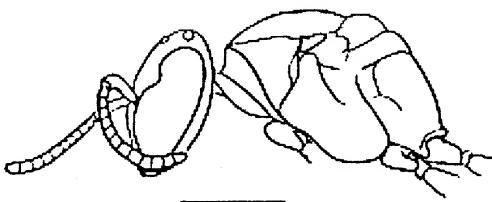
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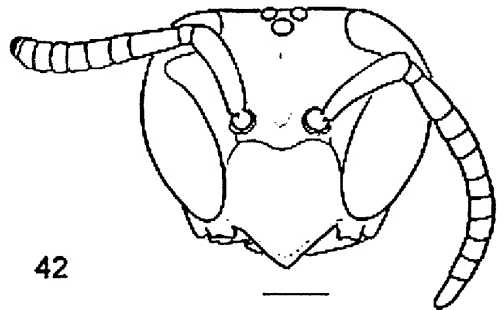
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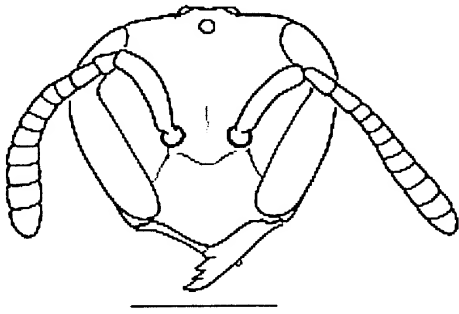


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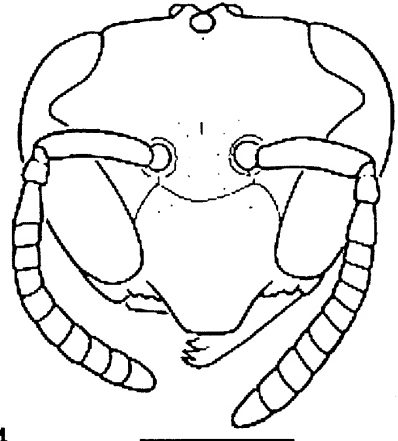


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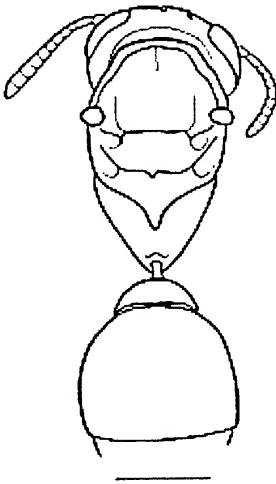
Figs. 37–42. Neotropical Polistinae. 37. *Polybia bistrata* (Fabricius), head in frontal view. 38–39. Hindwing. 38. *Apoica pallens* (Fabricius). 39. *Agelais multipicta* (Haliday), hindwing. 40–41. lateral view. 40. *Angiopolybia obidensis* (Ducke). 41. *Protopolybia sedula* (de Saussure). 42. *Angiopolybia obidensis* (Ducke), head in frontal view. All scale bars are 1.0 mm.



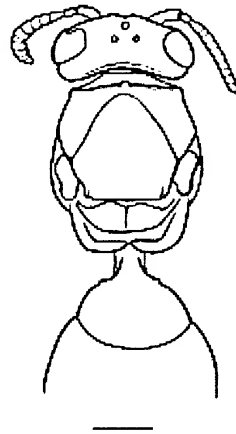
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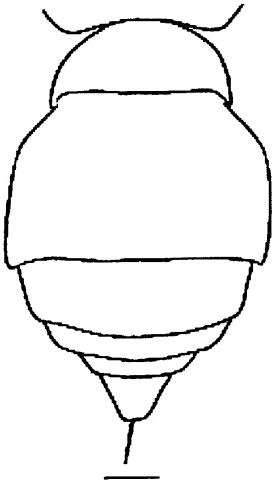
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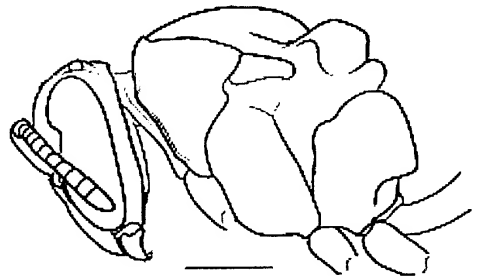
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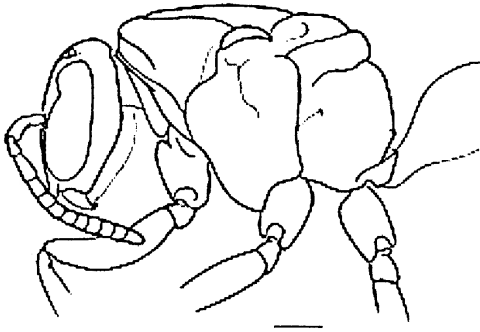


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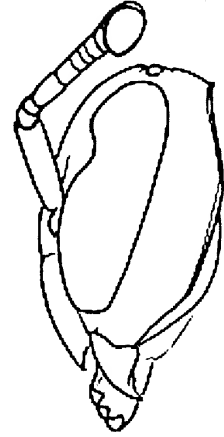


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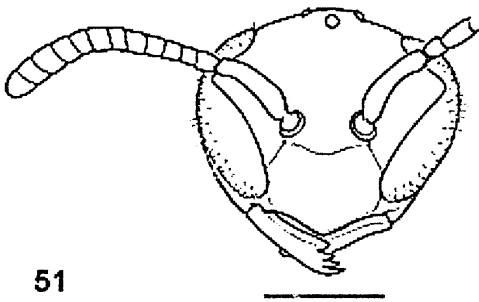
Figs. 43–48. Neotropical Polistinae. 43–44. Head in frontal view. 43. *Protopolybia sedula* (de Saussure). 44. *Charterginus fulvus* Fox. 45–46. Dorsal view. 45. *Protopolybia sedula* (de Saussure). 46. *Charterginus fulvus* Fox. 47. *Polybia depressa* (Ducke), metasoma in dorsal view. 48. *Charterginus fulvus* Fox, head and mesosoma in lateral view. All scale bars are 1.0 mm.



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Figs. 49–51. Neotropical Polistinae. **49.** *Polybia depressa* (Ducke), head and mesosoma in lateral view. **50.** *Protonectarina sylveirae* (de Saussure), head in lateral view. **51.** *Protonectarina sylveirae* (de Saussure), head in frontal view. All scale bars are 1.0 mm.

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REFERENCES

Bequaert, J.C. 1938. A new *Charterginus* from Costa Rica, with notes on *Charterginus*, *Pseu-*

dochartergus, *Pseudopolybia*, *Epipona*, and *Tatua* (Hymenoptera, Vespidae). *Revista de Entomologia* (Rio de Janeiro) 9: 99–117.

Bequaert, J.C. 1944. The social Vespidae of the Guianas, particularly of British Guiana. *Bulletin of the Museum of Comparative Zoology* 94: 249–300.

Carpenter, J.M. 1991. Phylogenetic relationships and the origin of social behavior in the Vespidae. In K.G. Ross and R.W. Matthews (editors), *The social biology of wasps: 7–32*. Ithaca, NY: Cornell University Press.

Carpenter, J.M. 1996. Phylogeny and biogeography of *Polistes*. In S. Turillazzi and M.J. West-Eberhard (editors), *Natural history and evolution of paper-wasps: 18–57*. Oxford: Oxford University Press.

Carpenter, J.M. 1999. Taxonomic notes on paper wasps (Hymenoptera: Vespidae; Polistinae). *American Museum Novitates* 3259: 1–44.

- Carpenter, J.M., J. Kojima, and J.W. Wenzel. 2000. *Polybia*, paraphyly and polistine phylogeny. *American Museum Novitates* 3298: 1–24.
- Carpenter, J.M., and J.W. Wenzel. "1989" [1990]. Synonymy of the genera *Protopolybia* and *Pseudochartergus* (Hymenoptera: Vespidae; Polistinae). *Psyche* 96: 177–186.
- Carpenter, J.M., J.W. Wenzel, and J. Kojima. 1996. Synonymy of the genus *Occipitalia* Richards, 1978, with *Clypearia* Saussure, 1854 (Hymenoptera: Vespidae; Polistinae, Epiponini). *Journal of Hymenoptera Research* 5: 157–165.
- Ducke, A. 1904. Sobre as Vespidas sociaes do Pará. *Boletim do Museu Goeldi* 4: 317–374.
- Ducke, A. 1905a. Nouvelles contributions à la connaissance des Vespides sociaes de l'Amérique du Sud. *Revue d'Entomologie* 24: 5–24.
- Ducke, A. 1905b. Sobre as Vespidas sociaes do Pará. (I.º. Supplemento). *Boletim do Museu Goeldi* 4: 652–698.
- Ducke, A. 1914. Über Phylogenie und Klassifikation der sozialen Vespiden. *Zoologischen Jahrbüchern, Abteilung für Systematik, Geographie und Biologie der Tiere* 36: 303–330.
- Fox, W.J. 1898. Contributions to the knowledge of the Hymenoptera of Brazil. No. 5. Vespidae. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1898: 445–460.
- Gribodo, G. "1891" [1892]. Contribuzioni imenoterologiche. Sopra alcune specie nuove o poco conosciute imenotteri diplotteri. Nota IV. *Bollettino della Società Entomologica Italiana* 23: 242–300.
- Guérin-Meneville, F.E. 1831. Crustacees, Arachnides et Insects. In L.I. Duperrey, *Voyage autour du monde sur la Coquille (1822–25)*. *Zoologie* 2(2), div. 1 pls. 8–9. Paris.
- Ihering, H. von. 1896. Zur Biologie der socialen Wespen Brasiliens. *Zoologischer Anzeiger* 19: 449–453.
- Ihering, R. von. 1904. As vespas sociaes do Brasil. *Revista do Museu Paulista* 6: 97–309.
- Ihering, R. von. 1913. O genero *Parachartergus* R. v. Ih. (vespas sociaes). *Revista do Museu Paulista* 9: 226–228.
- International Commission on Zoological Nomenclature. 1976. Opinion 1051. *Rhopalidia* Lepelletier, 1836 (Insecta: Hymenoptera): Suppressed under the plenary powers. *Bulletin of Zoological Nomenclature* 32: 240–241.
- Kirby, W. 1826. In W. Kirby and W. Spence, *An introduction to entomology, or elements of the natural history of insects* 3(1). London: Longman, Hurst, Rees, Orme, and Brown.
- Kojima, J. 1997. Abandonment of the subgeneric concept in the Old World polistine genus *Ropalidia* Guérin-Méneville, 1831 (Insecta: Hymenoptera: Vespidae). *Natural History Bulletin of Ibaraki University* 1: 93–106.
- Latreille, P.A. 1802. *Histoire naturelle, générale et particulière des Crustacées et des Insectes*. Paris: Sonnini's Suites à Buffon.
- Lepelletier de St. Fargeau, A.L.M. 1836. *Histoire Naturelle des Insectes. Hyménoptères, I*. Paris: Roret's Suites à Buffon.
- Möbius, K.A. 1856. Die Nester der geselligen Wespen. Beschreibungen neuer Nester—und einiger neuen Wespen-arten des naturhistorischen Museums zu Hamburg nebst Betrachtungen über den Nesterbau im Allgemeinen. *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 3: 117–171, 19 pls.
- Perty, M. 1833. *Delectus Animalium Articulatorum quae Itinere per Brasiliam—Collegerunt Dr. J. de Spix et Dr. C.F. Ph. de Martius*, fasc. 3. München.
- Raw, A. 1985. *Asteloecca*, a new neotropical wasp genus (Hymenoptera, Vespidae). *Revista Brasileira de Entomologia* 29: 185–188.
- Richards, O.W. 1941. The classification of the genus *Mischocyttarus* Saussure (Hymenopt., Vespidae). *Proceedings of the Royal Entomological Society of London (B)* 10: 124–130.
- Richards, O.W. 1978. The social wasps of the Americas, excluding the Vespinae. London: British Museum (Natural History).
- Richards, O.W., and M.J. Richards. 1951. Observations on the social wasps of South America (Hymenoptera, Vespidae). *Transactions of the Royal Entomological Society of London* 102: 1–170.
- Saussure, H. de. 1852. Note sur un nouveau genre de guêpes. *Annales de la Société entomologique de France* (2) 10: 549–556.
- Saussure, H. de. 1853–1858. *Monographie des guêpes sociales ou de la tribu des vespiciens*. Paris: Masson, and Genève: J. Cherbuliez.
- Saussure, H. de. 1863. *Mélanges Hyménoptérologiques. II. Vespides. Mémoires de la Société de Physique et d'Histoire naturelle de Genève* 17: 171–244.
- Vecht, J. van der. 1966. The East Asiatic and Indo-Australian species of *Polybioides* du Buysson and *Parapolybia* de Saussure (Hym., Vespidae). *Zoologische Verhandlungen* 82: 1–42.
- Wenzel, J.W. 1998. A generic key to the nests of hornets, yellowjackets, and paper wasps worldwide (Vespidae: Vespinae, Polistinae). *American Museum Novitates* 3224: 1–39.
- Wenzel, J.W., and J.M. Carpenter. 1994. Comparing methods: Adaptive traits and tests of adaptation. In P. Eggleton and R.I. Vane-Wright (editors), *Phylogenetics and Ecology*: 79–101. London: Academic Press.
- White, A. 1841. Description of a South American wasp which collects honey. *Annals and Magazine of Natural History* 7: 315–322.